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Nam Lot (MIS 5) and Duoi U'Oi (MIS 4) Southeast Asian sites revisited: Zooarchaeological and isotopic evidences

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ABSTRACT

The Nam Lot site in Laos and the hominin-bearing Duoi U'Oi site in Vietnam are dated to MIS 5 (86–72 ka) and MIS 4 (70–60 ka), respectively. Located in the same latitudinal belt ~20°N in the north of the Indochinese area, the faunal assemblages recovered from breccia deposits in a karstic context have the potential to provide information on the palaeoenvironmental conditions faced by earliest modern humans when they entered the Southeast Asian mainland. Here, zooarchaeological evidence of faunas are reviewed combined with a new stable isotope analysis ($\delta^{13}C$ and $\delta^{18}O$) of tooth enamel of mammals from Nam Lot (86–72 ka), to explore environmental conditions during MIS 5–4 periods.

In both sites, large predators (hyena, tiger, leopard, and dhole) had access to a great diversity of prey among mammals. The Nam Lot isotopic results indicate during MIS 5 a complexity in the forest habitats with closed low-light tropical rainforest, "intermediate" rainforest, and C_3–C_4 open woodland/'savanna'. This woodland ecosystem – notably the "intermediate" rainforest – carried most of the ungulate biomass, with a variety of small to large-bodied ground-dwelling animals.

1. Introduction

The debate surrounding the timing of early modern *Homo sapiens* arrival in Southeast Asia has shifted recently to the time range of ~120–70 thousand years ago [ka] in Marine Isotope Stage [MIS] 5 (Reyes-Centeno, 2016; Bae et al., 2017; Rabett, 2018). Indeed, archaeological and fossil data show that there is little doubt today that humans expanded from Africa towards Asia during the earliest stages of MIS 5, through the Arabian Peninsula to Southeast Asia, and adapting to various habitats along multiple routes, including inland vegetation corridors, coastal routes and riverine corridors (Field and Lahr, 2005; Mellars, 2006a, 2006b; Mellars et al., 2013; Field et al., 2007; Armitage

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et al., 2011; Oppenheimer, 2012; Boivin et al., 2013; Reyes-Centeno, 2016; Corny et al., 2017; Bae et al., 2017; Rabett, 2018). If the apparently concomitant arrival of *Homo sapiens* associated with a modern fauna around 120 ka at Punung in Java needs to be verified (Storm et al., 2005; Storm and de Vos, 2006; Westaway et al., 2007), other data from southern China (Zhiren, 116–106 ka, Liu et al., 2010a; Cai et al., 2017; Huanglong, 100–80 ka, Liu et al., 2010b; Shen et al., 2013; Luna, 126.9–70.2 ka, Bae et al., 2014; Longtanshan, > 83–60 ka, Curnoe et al., 2016) witness the presence of anatomically modern humans and other forms described as transitional in this time interval, whereas the Fuyan fossils (120–80 ka, Liu et al., 2015) appear highly controversial (Michel et al., 2016). In relation to MIS 4 (Periglacial Stage, ~71–52 ka), evidence come from the recently reconsidered age of the Lida Ajer site in Sumatra with one clearly identified *Homo sapiens* tooth (73–63 ka, Westaway et al., 2017), combined with the newly recovered *Homo sapiens* at Tam Pà Ling [TPL] from northeastern Laos ~70 ka (Demeter et al., 2017; Shackelford et al., 2018). By 65 ka, modern humans had already reached northern Australia (Clarkson et al., 2017). While we are not sure if archaic hominins were present in mainland SE Asia until the appearance of modern humans, archaic populations either related to *Homo erectus* or to a still unknown early *Homo* ancestor appear to be present in Java (Yokoyama et al., 2008; Indriati et al., 2011), in Flores (Sutikna et al., 2016), and maybe in the Philippines (Mijares et al., 2010) until c. 100 to 50 ka.

Determining the palaeoenvironmental conditions that the earliest modern humans faced when they entered the Southeast Asian mainland around the MIS 5–4 transition is an important issue that has been for the moment only poorly addressed. Human and large mammalian fossils we discovered in the north of Indochina come from various depositional contexts in tropical karst sites. In northern Vietnam and Laos, the only available MIS 5 data for reconstructing the habitats based on large mammals were derived from breccia deposits. Two sites located at the foot of the Pà Hang Mountain have yielded faunal assemblages, Tam Hang South (92–60 ka; Bacon et al., 2008a, 2011, 2015) and Nam Lot (86–72 ka; Bacon et al., 2012, 2015). In relation to MIS 4, findings come from clay layers that filled the TPL cave, located at the summit of the same Pà Hang Mountain. The stratigraphic sequence of TPL reveals, in itself, the possibility of different human populations arriving during MIS 4–3. The youngest remains at 46 ± 4 ka (OSL) consist of the TPL1 cranium with fully modern traits and the TPL2 mandible with a mixture of modern and archaic traits (Demeter et al., 2012, 2015). Recently, a new fossil, a partial mandible (TPL3) and a rib (TPL4), has been added to these discoveries, pushing the occupation of the site back to 70 ± 8 ka (IRSL) (Shackelford et al., 2018). This latter fossil is a reliable indicator that modern *Homo sapiens* occupied inland sites ~70 ka, but there is no direct faunal evidence - only a handful of isolated teeth of large mammals - associated with the human remains at the site. In contrast, we found a rich mammalian fauna in breccia deposits from a contemporaneous site, Duoi U'Oi in northern Vietnam (70–60 ka; Bacon et al., 2008b, 2015), located ~100 km apart from Pà Hang.

With the current state of knowledge, available data provide a generalized overview of the ecosystems of Indochina. On a continental scale, at the latitudes ~20°N, sedimentological and palynological records of the Leizhou Peninsula (Zheng and Lei, 1999), showed that the MIS 5 period (~128–71 ka) was marked by a warm climate, with temperatures ~2 °C warmer than during the Holocene and a vegetation cover dominated by a fagaceous monsoon evergreen forest. The shift from MIS 5 to MIS 4 was characterized by the increase of temperate elements (the monsoon forest was replaced by high-elevation vegetation; the montane forest reached down to the lowland by at least 600 m), under cool and relatively wet conditions (with ~4 °C cooler temperatures than present). At that time, the continent was inhabited by diversified faunas with terrestrial, semi-arboreal and arboreal species. The structure of these tropical forest ecosystems was particularly shaped by the presence of numerous large-sized herbivores > 250 kg (bovid, rhinoceros, and tapir), and very large-sized herbivores (megaherbivores > 1000 kg up to 5000 kg, Owen-Smith, 1988) (*Stegodon*, elephant, and giant tapir) (Wang et al., 2007; Rink et al., 2008; Bacon et al., 2018).

On a regional scale, palaeoenvironmental data need to be specified. In northeastern Laos (TPL, Tam Hang and Nam Lot), the nature of the forest cover is still unknown, while palynological results from northern Vietnam (Duoi U'Oi) provided sporadic data (Bacon et al., 2008b). The impacts of climate change at the MIS 5–4 transition on the biodiversity of megaherbivore-bearing ecosystems, and on the distribution and structure of the vegetation, remain to be assessed.

Beyond the scarcity of evidence in the Southeast Asian mainland, another major constraint for analyzing the evolution of hominins and their habitats is the representation of remains and their state of preservation which make the identification of hominin species difficult (Demeter et al., 2004, 2005; Liu et al., 2010b; Bae et al., 2014; Curnoe et al., 2016). Nam Lot (86–72 ka) has provided one isolated incisor assigned to a hominin (*Homo* sp.), but the possibility that it may belong to *Pongo* could not be fully ruled out either. Duoi U'Oi (70–60 ka) has provided two isolated molars assigned more securely to an unidentified hominin (*Homo* sp.) (Bacon et al., 2008b).

In this issue, stable isotope analysis is used increasingly to gain insights into past and present environments and animal ecology. $\delta^{13}C$ values of mammal tissues reflect the isotopic composition of ingested and assimilated food and can furthermore be used to reveal characteristics of ecology and environment (DeNiro and Epstein, 1978; Lee-Thorp et al., 1989; Ambrose and Norr, 1993; Cerling and Harris, 1999; Kohn and Cerling, 2002; Sponheimer et al., 2003; Passey et al., 2005). Consequently, plants' isotopic composition is reflected in every consumer's values - even carnivores' - since they constitute the primary sources of carbon in food webs. In tropical and subtropical regions, the flora is composed of plants using C_3 and C_4 photosynthetic pathways (Still et al., 2003), which $\delta^{13}C$ values vary markedly (Smith and Epstein, 1971). While C_3 plants dominate the terrestrial vegetation biomass (Still et al., 2003), including that of tropical forests (Ehleringer and Monson, 1993), C_4 plants are mostly restricted to tropical and subtropical regions as they require considerable levels of light and high temperature during their growing season (Ehleringer and Monson, 1993; Tieszen et al., 1997; Sage et al., 1999; Still et al., 2003). In the context of tropical forest, these distinctions have been used in Africa (e.g., White et al., 2009; Lee-Thorp et al., 2010; Sponheimer et al., 2013; Levin et al., 2015) and South Asia (e.g., Krigbaum, 2003, 2005; Roberts et al., 2015, 2017a) to assess the degrees of faunal and human reliance on forest resources dominated by C_3 plant taxa as opposed to open habitats where both C_3 and C_4 plant resources are available. Moreover, more subtle distinction in $\delta^{13}C$ of carbon sources linked to the "canopy effect" also exists within tropical C_3 forest ecosystems (van der Merwe and Medina, 1991). In Asia, the combined analysis of oxygen and carbon stable isotopes provided direct evidence of human rainforest adaptation from the Late Pleistocene to the Neolithic (Krigbaum, 2003, 2005; Roberts et al., 2015, 2017a). $\delta^{18}O$ measured in tooth enamel mostly reflects the isotope composition of ingested water (drinking and food) (Longinelli, 1984; Luz et al., 1984; Bryant and Froelich, 1995). In plants, $\delta^{18}O$ is related to soil water absorbed, which in turn derives from meteoric water that varies primarily according to the latitude and climate (Dansgaard, 1964; Longinelli, 1984). Within tropical and subtropical regions, $\delta^{18}O$ values can also be used, along with $\delta^{13}C$ values, to infer canopy density in a forest environment (Buchmann et al., 1997; Buchmann and Ehleringer, 1998).

In this paper, we focus the analysis on the two sites: Nam Lot (MIS 5: 86–72 ka) and Duoi U'Oi (MIS 4: 70–60 ka) located in the same latitudinal belt ~20°N. First, zooarchaeological evidences are reviewed to estimate the diversity of potential resources exploitable by predators (carnivores and/or hominins) among ground-dwelling, semi-arboreal, and arboreal mammals. These approaches were combined with a new stable isotope analysis ($\delta^{13}C$ and $\delta^{18}O$) of tooth enamel of mammals from Nam Lot (86–72 ka) for which the material was available for

Fig. 1. Map of the Southeast Asian mainland with the location of the studied Laotian and Vietnamese sites indicated by the black triangles.

sampling. $\delta^{18}O$ values are used to provide additional palaeoecological information related to $\delta^{13}C$ values.

2. Materials and methods

2.1. Presentation of the sites and mammalian assemblages

Nam Lot is an upland site located along the basal part of the Pà Hang Mountain at an elevation of 1120 m in northeastern Laos, Hua Pan province (Arambourg and Fromaget, 1938; Fromaget, 1940a, 1940b) (Figs. 1, 2). We discovered in the Nam Lot cave an assemblage of 385 isolated teeth (NISP) of mammals during the field season of 2007 (Duringer et al., 2012) (Fig. 3, Table 1SI). The majority of remains were derived from the breccia and from the silty to sandy clays in the lower part of the cave, which has an estimated age range of 86–72 ka (OSL and U-series; Bacon et al., 2015).

The Nam Lot fauna is composed of middle- to large-sized mammals (Artiodactyla, Perissodactyla, Proboscidea, Carnivora, Primates, and large Rodentia), whereas the whole category of small mammals and microvertebrates are lacking due to postburial processes in the karsts (Bacon et al., 2015). Compared to the species diversity in living faunas from regions situated at the same northern latitudes (0°–25°) (Corbet and Hill, 1992), Artiodactyla (five identified species among seven taxa) show remarkable similarities, whereas Perissodactyla and Proboscidea (six identified taxa at the species and genus level) show a number of species twice greater. The diversity in Carnivora species is largely underestimated - eight well-identified species are recorded at Nam Lot - considering the 21 to 29 species inventoried in the living faunas in the northern latitudes. In relation to small-sized Primates, the assessment of species diversity remains limited due to the fact that most identifications could only be made at the genus level (Bacon et al., 2015).

The Duoi U'Oi lowland site, located around 100 km away from the

Fig. 2. Photo of the Pà Hang Mountain in northeastern Laos.

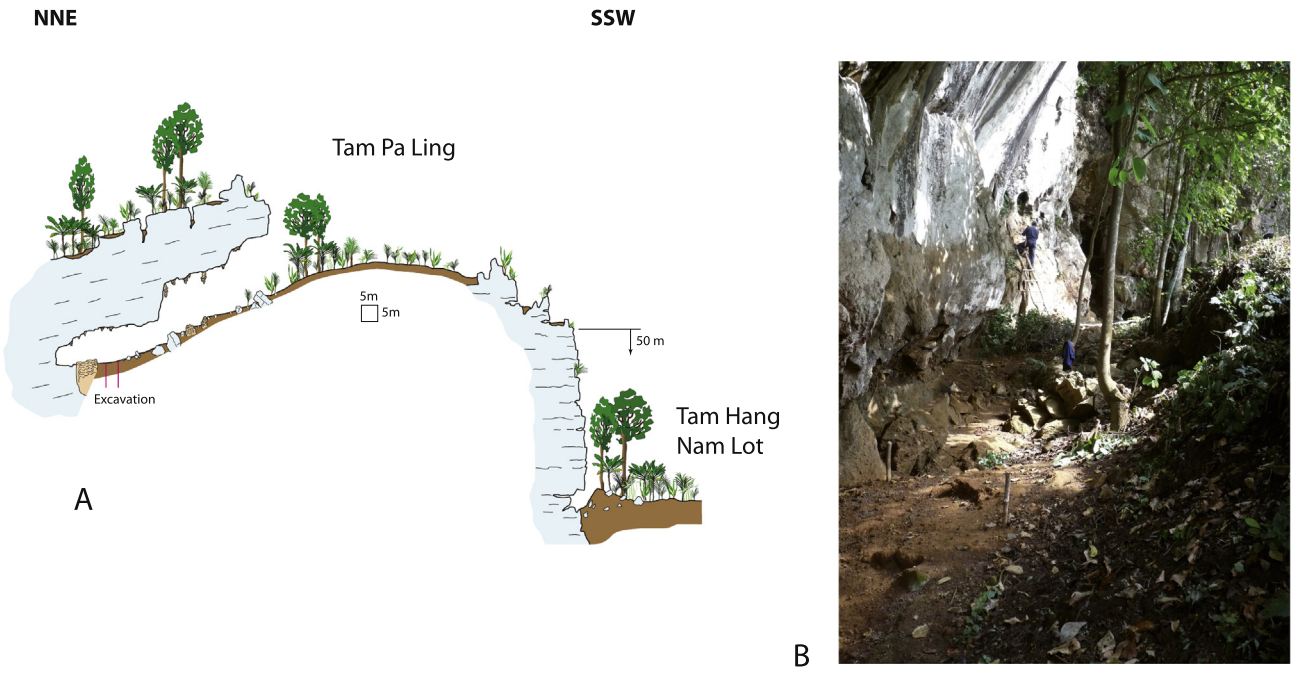

Fig. 3. A. Section of the Pà Hang Mountain showing the location of the different localities. The fossil-bearing site includes various depositional contexts: the silty to sandy clay layers of the Tam Pà Ling cave at an elevation of 1170 m, and the breccia deposits of the Nam Lot cave and Tam Hang South rock shelter located along the cliff of the Mountain at an elevation of 1120 m; B. Photo of the basal part of the Pà Hang cliff.

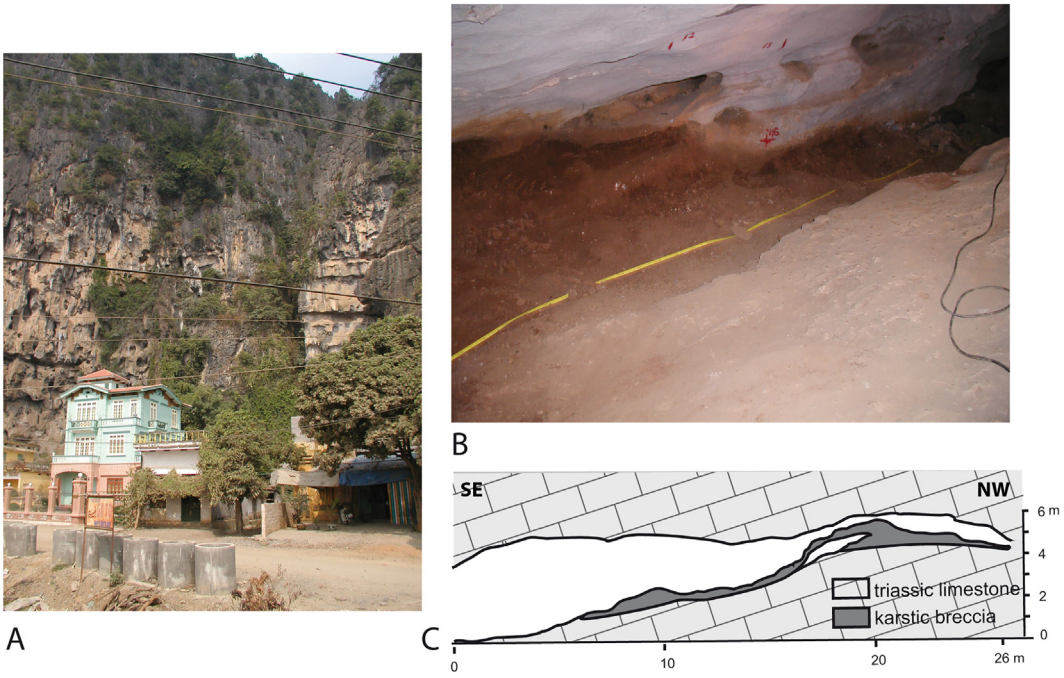

Fig. 4. Location and stratigraphic context of the Duoi U'Oi breccia deposits. A. The entrance of the cave is situated behind houses at the level of the alluvial plain (3 m above the alluvial plain); B. All teeth (fauna and hominins) come from one well-preserved calcareous to argillaceous breccia located along the wall of one corridor (corridor 1, Bacon et al., 2008b); C. Section of the corridor 1.

Pà Hang Mountain (Fig. 1), yielded an assemblage of 871 isolated teeth (NISP) of mammals (Table 1SI). The cave is situated around 3 to 5 m above the level of the alluvial plain and all teeth come from one well-preserved calcareous to argillaceous breccia located along the wall of the only excavated corridor (Fig. 4) (Bacon et al., 2008b). Considering the processes of transport through the cave system and the formation of the breccia, the fossiliferous layer formed within a relatively short time period during a unique depositional event (only one phase of stagnation with no reworking and redeposition). The estimated age of the fauna (70–60 ka) is based on luminescence dating of the underlying sandy and silty clay unit and U-series dating of the calcitic floor (66 ± 3 ka) that crosses the fossiliferous breccia (Bacon et al., 2015).

In terms of preservation of remains, the Duoi U'Oi fauna is similar to that of Nam Lot with only middle- to large-sized mammals. In

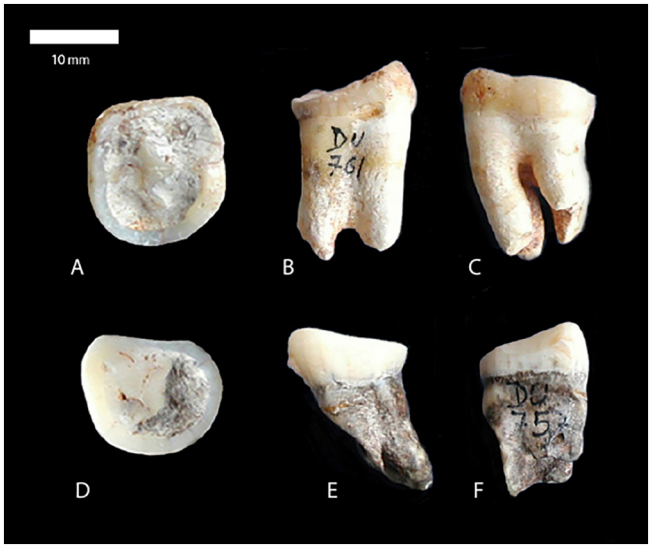

Fig. 5. The two hominin Duoi U'Oi teeth (70–60 ka, Vietnam). Contrary to the initial description (Bacon et al., 2008b), the DU761 specimen represents a mandibular molar and not a maxillary molar. Upper row: right lower m1 (DU761) in occlusal (A), buccal (B), and lingual (C) views; lower row: right upper M3 (DU757) in occlusal (D), buccal (E), and lingual views (F).

comparison with the species diversity in living faunas from the region (Corbet and Hill, 1992), Artiodactyla (six species) are well represented, whereas Perissodactyla and Proboscidea are much more numerous (seven taxa among which four identified species). In contrast, both the species diversity in Carnivora and Primates species are underestimated due to various biases (Bacon et al., 2015). At Duoi U'Oi, two *Homo* molars have been recognized by using dimensions and morphological criteria observed on the surface of crowns and roots (Bacon et al., 2008b). The teeth are heavily worn and it was impossible to assign them to any species (*H. sapiens* or *H. erectus* or another hominin) (Fig. 5).

Despite the poor preservation and rarity of pollen grains, the palynological analysis of the Duoi U'Oi sediments revealed a mixture of warm and temperate elements (Fig. 2SI). Of the components of the vegetation, 31% are pollen grains of non-arboreal plants and abundant Poacae, 25% are fern spores with diverse species, and 8% are arboreal and shrub plants.

In both sites, the taphonomic analysis revealed that porcupines were the main accumulator agent before burial in the sediments (Bacon et al., 2015). The behavior of porcupines in accumulating a wide range of remains of predated or scavenged animals by either Carnivora or hominins, suggests that assemblages can be used as indicators of abundance of mammals living in the areas surrounding the sites, and therefore prey-preference by predators (Brain, 1981).

2.2. Methods

2.2.1. Stable isotopic background

The $\delta^{13}C$ values in the bioapatite, which constitutes the bone and enamel of the tooth of a consumer, reflect those of its diet (DeNiro and Epstein, 1978; Lee-Thorp et al., 1989; Sponheimer and Lee-thorp, 1999; Cerling and Harris, 1999; Passey et al., 2005). Enamel is metabolically inert after formation. It thus only records the isotopic composition of the diet consumed during the period of its formation and maturation. It is not sensitive to post-mortem alteration and contamination and can thus be used to provide valid palaeodietary and palaeoenvironmental information (Lee-Thorp et al., 1989; Sponheimer and Lee-thorp, 1999; Cerling and Harris, 1999; Kohn and Cerling, 2002).

The basis for estimating the reliance on food resources is the existence of "isotopically" distinct - and relatively invariant over time - resources in the environment, such as plants using C_3 and C_4 photosynthetic pathways (Smith and Epstein, 1971; O'Leary, 1981; Farquhar et al., 1989). C_3 plants dominate the terrestrial vegetation and are composed of trees, bushes, shrubs and grasses while C_4 plants, mainly composed of grasses and sedges, occur primarily in the vast tropical and subtropical grassland and savanna regions as well as in temperate grassland regions in North and South America and Africa (Still et al., 2003). $\delta^{13}C$ values range from −37‰ to −20‰ with an average value of about −27‰ for C_3 plants (Kohn, 2010), and −17‰ to −10‰ with an average value of about −12.5‰ for C_4 plants (Smith and Epstein, 1971; O'Leary, 1988). The range of $\delta^{13}C$ values of C_3 plants is large but extreme values are found in particular contexts. Values lower than −31.5‰ are only found for vegetation growing under a heavy forest cover in tropics (Kohn, 2010), a phenomenon known as "canopy effect". These low $\delta^{13}C$ values are caused by 1) decreasing light and photosynthetic rates, 2) increasing humidity and recycling of soil-respired CO_2, both according to decreasing height from the forest crown (Vogel, 1978; Ehleringer et al., 1986, 1987; Medina et al., 1986; Sternberg et al., 1989; van der Merwe and Medina, 1989; Graham et al., 2014). As a consequence, there is a trend in decreasing values with decreasing canopy height but this effect can be confounded by plant parts (Roberts et al., 2017b). A marked distinction in $\delta^{13}C$ values can be nevertheless observed between vegetation from the densely forested areas and more open areas (e.g., Cerling et al., 2004, 2015; Levin et al., 2008; Blumenthal et al., 2016; Roberts et al., 2015, 2017a, 2017b). Vegetation values higher than −23‰ are only found in the Atacama Desert and for the *Pinus* genus in dry environments (Smith and Epstein, 1971; O'Leary, 1988; Ehleringer et al., 1998; Kohn, 2010). Therefore, a more restricted range of $\delta^{13}C$ values of −37‰ to −23‰ is considered for the studied geographic area.

Following the burning of fossil fuels over the past 150 years, the $\delta^{13}C$ of atmospheric CO_2 has decreased impacting the $\delta^{13}C$ of all living organisms. The $\delta^{13}C$ values of modern plants are then corrected (~1.5‰; Friedli et al., 1986) when compared to those of organisms dating back from before the atmospheric CO_2 shift. In the present study, the upper limit for C_3 plants is thus shifted from −23‰ to −21.5‰, and the lower limit for C_4 plants from −17‰ to −15.5‰.

Distinct isotopic signatures are transmitted to the consumer with a trophic fractionation when the food's carbon is incorporated into the tissues of animals (Lee-Thorp et al., 1989). The value of the fractionation varies according to the tissue (bone collagen, enamel carbonate, hairs, etc.) and, for the same type of tissue, according to animal biology and digestive physiology (herbivorous, carnivorous, and omnivorous) (Lee-Thorp et al., 1989; Passey et al., 2005). We applied an average spacing of +14‰ between diet and dental enamel bioapatite of herbivores (Lee-Thorp et al., 1989; Cerling and Harris, 1999; Passey et al., 2005). Although spacing range of +12–14‰ is mentioned in the literature for ungulates (Lee-Thorp and van der Merwe, 1987), a more widespread spacing value of ± +14‰ was considered more suitable in the present study (Cerling and Harris, 1999; Balasse, 2002; Passey et al., 2005). This choice is even more relevant considering that multiple diet-enamel spacing values were considered here, rather than a single one. Furthermore, as Nam Lot is located in low latitudes (< 40°N) within the tropics where herbaceous species are only of C_4 photosynthetic type (Prentice et al., 1992; Still et al., 2003; Kohn and Cerling, 2002), it is possible to discriminate between "grazers" that mostly eat grass and low vegetation and "browsers" that preferentially eat leaves and soft shoots.

An average enamel-diet spacing of +9‰ was established for carnivores (Lee-Thorp et al., 1989). However, the $\delta^{13}C$ values of dental enamel of carnivores are similar to those of their prey (Lee-Thorp et al., 1989) because the ingested and assimilated parts are soft tissues (muscles, fat, etc.) and not hard tissues. As such, a slightly negative value difference (−1.3‰) was established between the $\delta^{13}C$ values of dental enamel of the gray wolf (*Canis lupus*) and those of its prey (Fox-Dobbs et al., 2006). Although ursids are known to exhibit carnivore

diet-enamel spacing (Bocherens, 2002; Bocherens et al., 2011), their dietary reliance however is not necessarily restricted to meat consumption.

An average enamel-diet spacing of omnivores (pigs and porcupines) of +13‰ was established for pigs (Passey et al., 2005). Finally, the average enamel-diet spacing for primates is unclear and varies throughout the literature (e.g., Ambrose et al., 1997; Krigbaum, 2003; Cerling et al., 2004, 2013; Codron et al., 2005; Sponheimer et al., 2013). Following current evidence (Cerling et al., 2004; Sponheimer et al., 2013), an average conservative enamel-diet spacing of +13‰ has been used for primates for the present study.

The terms C_3 and C_4 refer to photosynthetic type plants and are adequate to describe the diet of herbivores. However, we will also use them for omnivores and primates, which can incorporate non-vegetable foods in their diets, as well as for carnivores. Therefore, in the present study, C_3 and C_4 terms also refer to the exploitation of resources provided from environment dominated by either C_3 or C_4 plants, and not to the consumption of plant per se. Using plants $\delta^{13}C$ values and enamel-diet spacing values, range of C_3, C_4 and mixed diets for herbivores, carnivores, omnivores and primates have been established and used to infer the Nam Lot palaeoenvironment according to faunal resource exploitation.

In homeothermic animals, the oxygen isotopic composition ($\delta^{18}O$) of tooth enamel is determined by the $\delta^{18}O$ value of body water, which is itself mainly influenced by drinking water and chemically-bound water in the diet (Longinelli, 1984; Luz et al., 1984; Bryant and Froelich, 1995; Kohn et al., 1996; Fricke et al., 1998a, 1998b). This in turn varies primarily according to the latitude and climate, where temperature, moisture content, amount of precipitation and isotopic composition of precipitation influence the $\delta^{18}O$ values of local water (Dansgaard, 1964; Longinelli, 1984; Kohn and Cerling, 2002). In tropical and subtropical regions, it has been shown that the $\delta^{18}O$ values of vegetation mostly reflect either evaporative potential or the source-effect of rainfall (Buchmann et al., 1997; Buchmann and Ehleringer, 1998; McCarroll and Loader, 2006).

As for $\delta^{13}C$ values, $\delta^{18}O$ can also be used to infer the density of a forest cover because of the canopy effect (Sternberg et al., 1989; Buchmann et al., 1997; Buchmann and Ehleringer, 1998). Flora and fauna living on the forest floor exhibit the lowest $\delta^{18}O$ and $\delta^{13}C$ values (van der Merwe and medina, 1991; Krigbaum, 2003; Krigbaum et al., 2013; Blumenthal et al., 2016; Roberts et al., 2017b). However, recent work demonstrated a lack of clear vertical $\delta^{13}C$ values height stratification in plants within the canopy (Blumenthal et al., 2016), while $\delta^{18}O$ values in vegetation, mostly leaves, are likely to be sensitive to a height gradient within and under the canopy (Sternberg et al., 1989; Cerling et al., 2004; Ometto et al., 2005; Krigbaum et al., 2013). This vertical gradient results in changing evaporative rate at different heights (Sternberg et al., 1989; Buchmann et al., 1997; Buchmann and Ehleringer, 1998; Ometto et al., 2005). However, it can be difficult in the absence of a local large dataset of tropical forest plants to distinguish low values caused by different evaporative rate rather than by different evaporative potential in plant parts (Roberts et al., 2017b). For example, leaf water will already exhibit higher $\delta^{18}O$ values compared to other parts of the same plant (Gonfiantini et al., 1965; Dongmann et al., 1974; Epstein et al., 1977; Sternberg et al., 1989; Yakir, 1992).

2.2.2. Tooth and enamel sample process

A total of 51 teeth belonging to 17 taxa (among which 12 at a species level) were selected for the isotopic analysis of the Nam Lot fauna. One to six specimens per species were used. Preparation started with a thorough cleaning of the surface and the removing of a superficial layer of enamel in order to remove any exogenous or contaminant material and thus ensuring the quality of further isotopic analysis. About 4 to 13 mg of enamel was obtained along the height of the crown of each tooth using a handheld Dremel® drill equipped with a diamond-tipped bur. Powdered enamel samples were soaked in a solution of 1 mL of 0.1 M/L acetic acid (CH_3COOH) for 4 h at room temperature in order to eliminate exogenous carbonates and then rinsed three times in distilled water. Samples were dried overnight at 65 °C.

Isotopic analyzes of pretreated enamel samples were performed at the "Service de Spectrométrie de Masse Isotopique du Muséum (SSMIM)" in Paris by a "Delta V Advantage" isotopic mass spectrometer coupled to a "Kiel IV Carbonate Device" chemical preparer (Thermo®). During each mass spectrometer run, eight analyses of the SSMIM internal laboratory standard (Marble LM) were performed for a total of forty measurements. The isotopic values of the internal laboratory standard ($\delta^{13}C = +2.13‰$ and $\delta^{18}O = -1.83‰$) are normalized to the international standard NBS-19 ($\delta^{13}C = +1.95‰$ and $\delta^{18}O = -2.20‰$), and its repetitive measurement served to correct those of carbonate enamel samples run at the same time. It also serves to determine the precision of the mass spectrometer precision ($\sigma(\delta^{13}C) = 0.03‰$; $\sigma(\delta^{18}O) = 0.06‰$). Homogeneity of the enamel samples was further estimated by the repeated analysis ($n = 5$) of two specimens (NL-63 and NL-65) and was ± 0.017‰ and ± 0.015‰ for $\delta^{13}C$ and ± 0.136‰ and ± 0.066‰ for $\delta^{18}O$, respectively. Both carbon and oxygen isotopic values are presented in delta "δ" notation expressed as deviation ‰ compared to the International Standard Vienna Pee Dee Belemnite (VPDB).

3. Results

3.1. Zooarchaeological data

Nam Lot (86–72 ka) data demonstrate that the MIS 5 ecosystem in northeastern Laos clearly differed from that of the present-day with a larger spectrum of large herbivores. The ecosystem supported a high ungulate biomass, at least five types of ground-dwelling animals weighing from ~250 kg up to ~5000 kg. The fauna records at least one rhinoceros species (900–2700 kg; Francis, 2008), one tapir (*Tapirus indicus*, 250–350 kg; Francis, 2008), the two proboscideans (*Elephas* sp., 3500–5000 kg; Francis, 2008) and *Stegodon orientalis* (3000–5000 kg; Schepartz and Miller-Antonio, 2010), and at least two large bovid species (700–900 kg; Francis, 2008).

The analysis of the assemblage indicates a high degree of species interactions (Bacon et al., 2015). The abundance and diversity in ungulate prey species most likely favoured the presence of large populations of carnivores, as suggested by the presence of group-living predators, the dhole (*Cuon alpinus*, 10–21 kg; Francis, 2008), and the spotted hyena (*Crocuta crocuta ultima*, 45–80 kg; Hayward, 2006). The age structure of pigs reveals the predominance of young and mature adult individuals (*Sus scrofa*, ~30–60 kg), which enters the prey-size category of both predators (Fig. 3SI). The age structure of rhinocerotids has a clear hyena-preyed signature (Fig. 4SI). At Nam Lot, hyena packs were efficient hunters and scavengers of rhinoceros calves, up to ~400 kg (Laurie, 1982).

The MIS 4 Duoi U'Oi fauna (70–60 ka) contained a great diversity in large-bodied ground-dwelling ungulates (cervids, bovids, and rhinocerotids) despite the absence of archaic species, *Megatapirus augustus* (up to 800 kg; Janis, 1984), and *Stegodon orientalis* (up to 5000 kg). The diversity of rhinoceroses is particularly notable with all three living Asian species recorded, *Rhinoceros sondaicus*, *R. unicornis* and *Dicerorhinus sumatrensis* (Antoine, 2012). What is striking is that the fauna is fully modern in its composition, and the chronology of the deposits (U-Th, 66 ± 3 ka) (Bacon et al., 2008b), strengthened by two independent age estimates (U-Th and OSL, 70–60 ka) (Bacon et al., 2015), suggests that these changes were established by MIS 4 locally.

At Duoi U'Oi, the leopard (*Panthera pardus*, 45–65 kg; Francis, 2008) and the tiger (*Panthera tigris*, 180–245 kg; Francis, 2008) coexisted with the group-living dholes (10–21 kg). In this rich ungulate community, the age structure of pigs seems to be biased towards mature adult individuals, and among them the largest ones were preyed upon (~200 kg) suggesting a tiger signature at the site (Karanth and

Sunquist, 1995). No clear selectivity could be emphasized in the age structure of rhinoceroses, a pattern reflecting the natural attrition on a population (caused by disease, malnutrition, and/or hominin and non-hominin predators) (Figs. 3, 4SI).

The evidence of potential hominin contribution to the accumulation of the sambar deer remains (*Cervus unicolor*, 180–260 kg; Francis, 2008) has been identified based on age-at-death distribution of the prey species, in the absence of any further evidence (cut marks on bones, differential conservation of skeletal elements, etc.) (Fig. 3SI) (Bacon et al., 2015). The predominance of prime-adult individuals and the absence of old individuals in the mortality pattern likely represent a selective hunting where hominins primarily focused on the prime-aged members of the herd (Steele, 2003). To that respect, this mortality pattern differs from that generated by the tiger. Indeed, the sambar deer is among the preferred prey of the tiger (Hayward et al., 2012), but among adult animals killed, old-aged individuals are usually present (Karanth and Sunquist, 1995). A recent analysis of a late Middle Pleistocene fauna from northern Vietnam (Coc Muoi, 148–117 ka; Bacon et al., 2018), only composed of non-hominin large predators (tiger and dhole), is consistent with this observation made in current Indian ecosystems. Indeed, in the Coc Muoi mortality profile of the sambar deer, the adult category is represented by both prime-aged and old-aged individuals. This profile illustrates a pattern of possible attritional hunting of tigers, according to the availability and chance encounter with the prey (Schaller, 1967).

Overall, the two MIS 5–4 faunas demonstrate that the mainland ecosystems at the latitudes ~21°N supported a large ungulate biomass. When considering MNI ungulates by body-size category - that may be considered as a good representation of hunted and/or scavenged carcasses of prey species accumulated at the sites - the percentages of animals > 176 kg are the highest (46.3% and 59.1% for Nam Lot and Duoi U'Oi, respectively) (Fig. 6). Comparatively, the medium (30–175 kg) and small (< 30 kg) categories are much less significant (Fig. 6, Table 2SI).

3.2. Carbon and oxygen stable isotopic data ($\delta^{13}C$ and $\delta^{18}O$) of the Nam Lot fauna

$\delta^{13}C$ results are presented in Table 3SI and Fig. 7. The 51 samples belonging to 17 taxa show $\delta^{13}C$ values ranging from −18.2‰ to +0.3‰. The Bovidae have the highest intra-taxon variation (13.8‰), and *C. crocuta* the smallest (0.1‰). Herbivores (n = 29) present values between −18.2‰ (*Stegodon* cf. *orientalis*) and + 0.3‰ (Bovidae indet.), carnivores (n = 8) between −15.3‰ (*U. thibetanus*) and −12.6‰ (*U. thibetanus*), omnivores (n = 9) between −14.1‰ (*S. scrofa* and *H. brachyura*) and −12.1‰ (*H. brachyura*), and primates (n = 5) between −14.8‰ (*Macaca* sp.) and −11.5‰ (*Macaca* sp.). The majority of individuals (90%; n = 46) exhibit values associated with the resource exploitation of a C_3 environment. Only a limited number of taxa exhibit values reflecting a C_4 diet (Bovidae indet. (n = 1) and *Cervus unicolor* (n = 2)) or a mixed diet C_3/C_4 (*Bubalus bubalis* (n = 1) and *Cervus unicolor* (n = 1)).

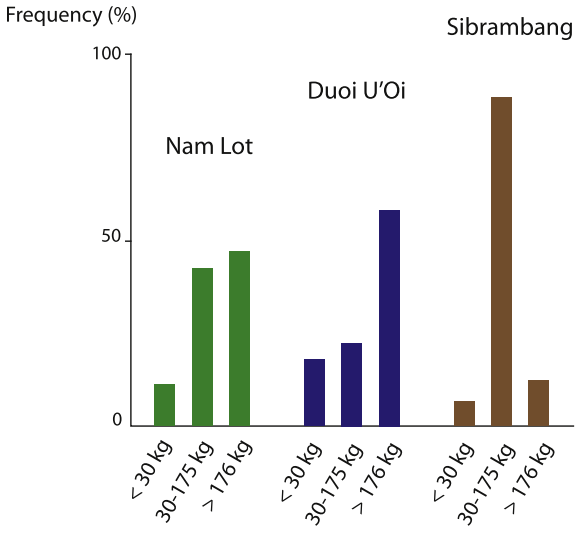

Fig. 6. MNI percentages by body-size category and age class (juvenile and adult) of ungulates in Late Pleistocene Southeast Asian faunas (modified from Bacon et al., 2015). The three body-size categories (small < 30 kg; medium 30–175 kg; large > 176 kg) are those used to study living populations by Karanth and Sunquist (1995).

The lowest end of Nam Lot faunal range, −18.2‰ to −14.0‰ (~41%, n = 21), is representative of closed low-light tropical rainforests (Cerling et al., 2004; Levin et al., 2008; Roberts et al., 2015, 2017a). Intermediate values, from −14.0‰ to −11.0‰ (~43%, n = 23), encompass the highest proportion of the specimens. These values can either reflect more open forest conditions similar to those of modern intermediate rainforests like Sri Lanka (annual rainfall of 1700–2200 mm) (Erdelen, 1988; Roberts et al., 2015, 2017a), or a mixed dietary reliance going from closed forests to open C_3 environments (e.g., Sponheimer et al., 2006; Levin et al., 2008; Roberts et al., 2015, 2017a). However, the taxa that exhibit $\delta^{13}C$ values between −18.2‰ and −11.0‰ include primates, rodents and other mammals that are known to prefer forest foraging. The majority of values found between −14.0‰ and −11.0‰ are thus likely to represent the acquisition of resources from a forest structure similar to that of modern intermediate rainforests rather than a mixed dietary reliance ranging from closed forests to open C_3 environments (Roberts et al., 2015, 2017a). A similar trend was first exposed at Balangoda Kuragala (~15,000 ± 3000 cal. years BP), Sri Lanka (Roberts et al., 2015, 2017a). Additionally, there is a striking contrast with taxa present in the highest end of the $\delta^{13}C$ range, −11.0‰ to +0.3‰ (~14%, n = 7). These three taxa (*B. bubalis*, Bovidae indet., and *C. unicolor*) are all known to show a great variability in their grazing behavior. $\delta^{13}C$ values of −11.0‰ to +0.3‰ are likely to stem from a variable contribution of C_4 resources present within a mixed forest/woodland/'savanna' C_3 environment (e.g. Cerling and Harris, 1999; Cerling et al., 2004, 2015; Sponheimer et al., 2006; Levin et al., 2008; Roberts et al., 2015, 2017a).

Large ungulates (*B. bubalis*, Bovidae indet., and *C. unicolor*) exhibit the highest variation in $\delta^{13}C$ values (−14.1‰ to +0.3‰), suggesting an opportunistic feeding behavior and habitat foraging from closed forest and intermediate rainforest to open grassland. Smaller ungulates and other ground-dwelling taxa (*C. sumatrensis*, *M. muntjak*, *S. scrofa*, and *H. brachyura*) display a more restricted isotopic range (−14.6‰ to −12.1‰) and most likely relied on open intermediate rainforests. Megaherbivores (*Tapirus* sp., *Elephas* sp., and *Stegodon*) with the exception of the rhinoceros ($\delta^{13}C$ values from −18.1‰ to −14.9‰) show a comparable reliance on exclusively closed low-light forest resources (−18.1‰ to −14.9‰). Although some individuals among rhinoceroses present values consistent to that of most megaherbivores, some others present higher values (−16.3‰ to −12.7‰) associated with open intermediate rainforests. This partitioning could be explained by the difference in dietary preference between different species, but not recognized here based on dental morphology. Primates (*Macaca* sp., and *P. pygmaeus*) $\delta^{13}C$ values (−14.8‰ to −11.5‰) fall within a similar range than that seen in Asia through the literature (e.g., Pushkina et al., 2010; Roberts et al., 2015, 2017a; Bocherens et al., 2017). When compared to extinct and extant specimens, Nam Lot giant pandas *A. melanoleuca* exhibit lower $\delta^{13}C$ values (−14.9‰ and −14.5‰) although still within the range of a diet composed of foodstuff (most likely bamboo) found in closed canopy environments (e.g., Stacklyn, 2016; Bocherens et al., 2017; Ma et al., 2017; Stacklyn et al., 2017). *U. thibetanus* exhibits low $\delta^{13}C$ values (−15.3‰ to −12.6‰), with some samples falling within the range of the lowest end of $\delta^{13}C$ values, attesting to a reliance on closed forest environments. Finally, *C.*

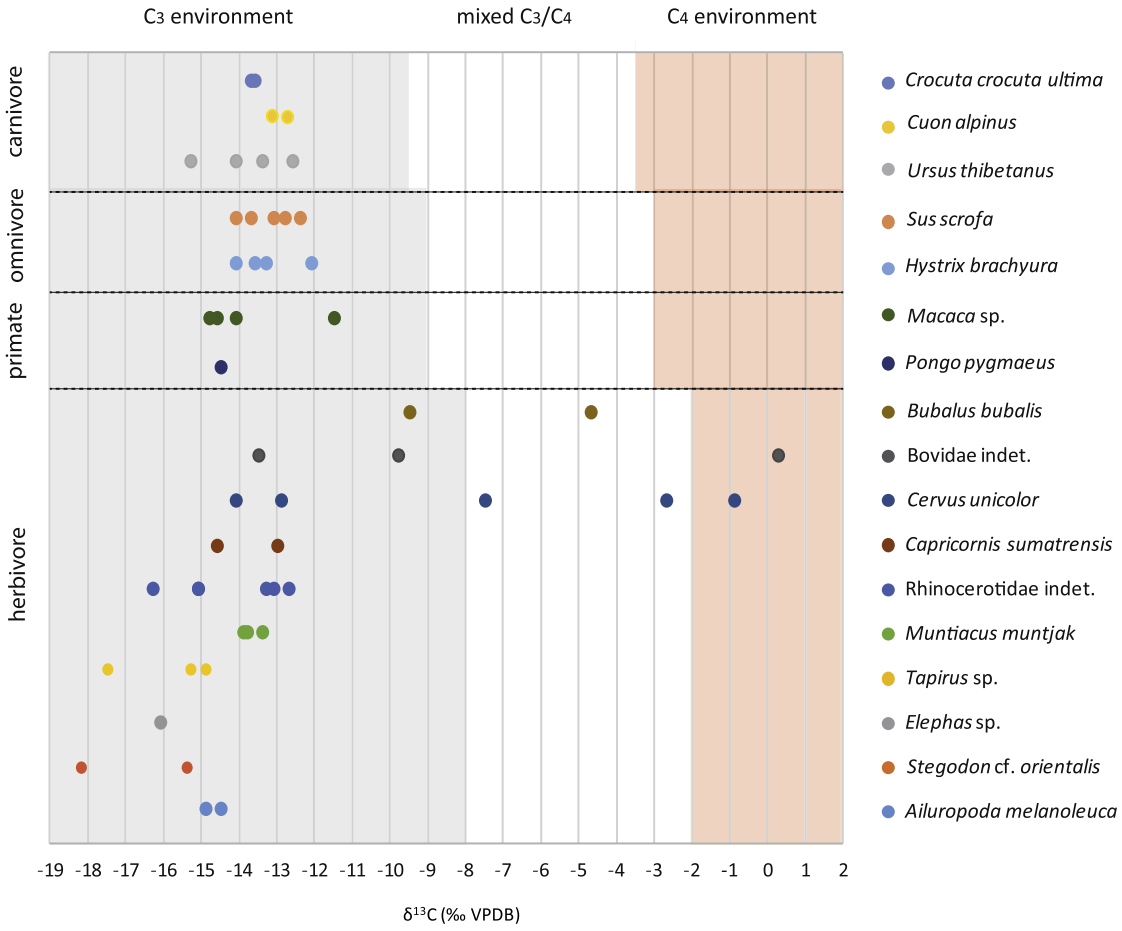

Fig. 7. Distribution of $\delta^{13}C$ values obtained within each taxon of the Nam Lot fauna. The following limits were established in order to differentiate the diets of the different individuals of herbivores: $C_3 = \delta^{13}C < -8.0‰$, mixed $= -8.0‰ > \delta^{13}C < -2.0‰$, $C_4 = \delta^{13}C > -2.0‰$ (Lee-Thorp et al., 1989; Cerling and Harris, 1999; Passey et al., 2005); carnivores: $C_3 = \delta^{13}C < -9.5‰$, mixed $= -9.5‰ > \delta^{13}C < -3.5‰$, $C_4 = \delta^{13}C > -3.5‰$ (Lee-Thorp et al., 1989; Fox-Dobbs et al., 2006); and omnivores and primates: $C_3 = \delta^{13}C < -9.0‰$, mixed $= -9.0‰ > \delta^{13}C < -3.0‰$, $C_4 = \delta^{13}C > -3.0‰$ (Passey et al., 2005; Cerling et al., 2004; Sponheimer et al., 2013).

crocuta ultima and *C. alpinus* both exhibit relatively low values (−13.7‰ to −13.0‰) that would result from the consumption of prey whose diet reflects intermediate rainforest foodstuff, or more likely the consumption of prey which relied on mixed vegetation, from closed forest to open C_3-C_4 environments.

$\delta^{18}O$ results are presented in Table 3SI and Fig. 8. $\delta^{18}O$ values range from −9.0‰ (*U. thibetanus*) to −2.5‰ (Rhinocerotidae indet.), *U. thibetanus* having the largest inter-individual amplitude (5.9‰), and *C. crocuta ultima* the smallest (0.3‰). Herbivores (n = 29) exhibit $\delta^{18}O$ values between −8.7‰ (*C. unicolor*) and −2.5‰ (Rhinocerotidae indet.), while those of carnivores (n = 8) vary from −9.0‰ (*U. thibetanus*) to −3.0‰ (*C. alpinus*). Both omnivores (n = 9) and primates (n = 5) have a narrower range of $\delta^{18}O$ values, between −6.8‰ (*S. scrofa*) and −5.2‰ (*H. brachyura*), and between −6.1‰ (*Macaca* sp., and *Pongo pygmaeus*) and −3.6‰ (*Macaca* sp.), respectively.

Unexpectedly, most large ungulates (*B. bubalis*, Bovidae indet., and *C. unicolor*) exhibit a somewhat narrow range of $\delta^{18}O$ values when compared to their respective range of $\delta^{13}C$ values. Indeed, a combination of relatively high $\delta^{18}O$ and $\delta^{13}C$ values could have been expected as a likely result of feeding and drinking in open C_4 environments. However, most of these individuals, which likely incorporated C_4 plants present values (−6.5‰ to −4.4‰; mean = −5.5 ± 0.7‰) close to the bulk of population $\delta^{18}O$ (mean = −5.7 ± 1.4‰). Likewise, the megaherbivores (*Tapirus* sp., *Elephas* sp., *S.* cf. *orientalis*, and Rhinocerotidae indet.) which display the lowest $\delta^{13}C$ values were consequently expected to display the lowest $\delta^{18}O$ values, following the same depletion trend of the canopy effect. With the exception of a single rhinoceros individual exhibiting a high $\delta^{18}O$ value (−2.5‰), they all nevertheless exhibit $\delta^{18}O$ values (−6.8‰ to −4.3‰; mean = −6.0 ± 0.9‰) close to that of the bulk of the population. The ground-dwelling *S. scrofa* and *H. brachyura* both display a similar and narrow range of $\delta^{18}O$ (−6.8‰ to −5.2‰), as does the *C. crocuta ultima* hyena, falling precisely within the bulk of population $\delta^{18}O$. Surprisingly, the $\delta^{18}O$ value obtained for the arboreal orangutan *P. pygmaeus* (−6.1‰) does not differ significantly from all of these previously mentioned ground-dwelling taxa. *Macaca* however displays mostly high $\delta^{18}O$ values (−6.1‰ to −3.6‰; mean = −4.6 ± 1.2‰). This dissimilarity in $\delta^{18}O$ values observed between the two primate taxa may be explained by dietary differences, and by the fact that macaques drink most likely more open water. Owing to different evaporative potentials, the chemically-bound water found in leaves exhibit higher $\delta^{18}O$ values compared to other parts of the same plant (Gonfiantini et al., 1965; Dongmann et al., 1974; Epstein et al., 1977; Sternberg et al., 1989; Yakir, 1992), resulting also possibly in the higher $\delta^{18}O$ values in macaques than in orangutans. All of the other taxa exhibit either relatively high $\delta^{18}O$ values (*C. sumatrensis*; −4.1‰ to −3.3‰) or a mix of both high and low $\delta^{18}O$ values (*M. muntjak*, *C. alpinus*, *U. thibetanus*, and *A. melanoleuca*; −8.3‰ to −3.0‰). These higher values result most likely in feeding and drinking behavior in more open C_3 environment, when compared to the bulk of population

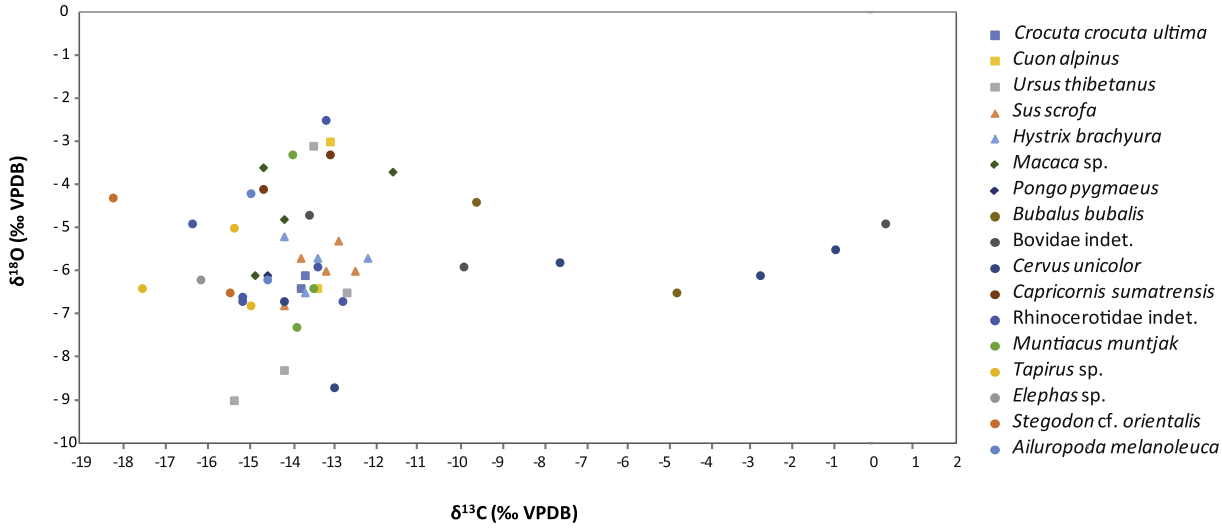

Fig. 8. Distribution of $\delta^{13}C$ and $\delta^{18}O$ values at the individual level for each taxon of the Nam Lot fauna.

$\delta^{18}O$.

As it is the case with the $\delta^{13}C$ values, a large range of $\delta^{18}O$ values can be observed at Nam Lot (−9.0‰ to −2.5‰) as already observed for other Asian sites (e.g., Pushkina et al., 2010; Roberts et al., 2015, 2017a; Bocherens et al., 2017). However, while most $\delta^{13}C$ values were consistent with known species behavior, diet and habitat preferences, $\delta^{18}O$ values are somewhat more complex to interpret. At the intraspecific level, such isotopic variability may be explained by variability in diet and drinking intakes (Bryant and Froelich, 1995; Kohn et al., 1996; Fricke et al., 1998a, 1998b; Kohn and McKay, 2012). The largest variability in $\delta^{18}O$ values, associated to $\delta^{13}C$ values showing dietary reliance on open forest or a mixed closed forest to open C_3 environment, could be linked to the large range of coexisting habitats at Nam Lot. An alternative explanation is a variation in the ^{18}O values of meteoric waters and environmental conditions over the deposition/accumulation time. As the faunal assemblage of Nam Lot is constrained between 86 and 72 ka, the variability in ^{18}O values could be the result of climatic changes, which occurred around 70 ka, during the termination of MIS 5. A larger dataset could help to elucidate the high intraspecific variations observed for $\delta^{13}C$ or $\delta^{18}O$ at Nam Lot and other Asian sites.

4. Discussion

4.1. MIS5 environmental context in northeastern Laos

The Nam Lot data provide a description of the palaeoenvironment during the terminal phase of MIS 5 (~128–71 ka). No reliable evidence supports for the moment the presence of modern humans during that period in the north of the Indochinese region.

The range of $\delta^{13}C$ values of animals is large with a strong predominance of C_3 resources in the diet (90%, n = 46), with very few taxa (e.g., large bovids and sambar deer) confidently exploiting C_4 resources (10%, n = 5). While $\delta^{18}O$ values cannot be fully explained yet, the variability in $\delta^{13}C$ and $\delta^{18}O$ values seen in the Nam Lot material is nevertheless consistent with that observed in other Asian sites (e.g., Pushkina et al., 2010; Roberts et al., 2015, 2017a; Bocherens et al., 2017), and most notably at Balangoda Kuragala and Batadomba-Lena (Roberts et al., 2015, 2017a) where similar palaeoecological trends can be observed.

Both zooarchaeological data and $\delta^{13}C$ values attest to the existence of a mosaic of habitats. Furthermore, the Nam Lot isotopic results bring insight and precision to the nature of the forest cover during the terminal phase of MIS 5 in northeastern Laos. $\delta^{13}C$ values indicate a complexity in the forest habitats with closed low-light tropical rainforests, "intermediate" rainforests, and C_3–C_4 open woodlands/'savannas'. This woodland ecosystem – notably the "intermediate" rainforest – carried most of the ungulate biomass, with a variety of small to large-bodied animals on the ground, including muntjac, wild pig, sambar deer, serow, wild cattle, and rhinoceros, which is strong evidence of a high primary productivity biomass with high production of edible plant material (Geist, 1974; Eisenberg and Seidensticker, 1976). In this ecosystem-type, tapir, elephant and *Stegodon* were particularly adapted to canopied woodlands, as also emphasized for southern Chinese ecosystems (Bocherens et al., 2017; Li et al., 2017; Ma et al., 2017).

The Nam Lot zooarchaeological and isotopic results also provide the first unequivocal evidence for the presence of open woodland and savanna zones at these latitudes (~20°N) during the MIS 5 warm and humid period. These zones most likely constituted a relatively attractive environment for predators. Open areas along watercourses or swamps and grassland are interesting habitats to forage, considering the need of abundant water for rhinoceroses and large cattle like buffaloes, and aptitude for most of the forest-living species, especially sambar, wild pig, and water buffalo, to gregariousness in open areas (Schaller, 1967; Eisenberg and Lockhart, 1972; Lekagul and McNeely, 1997; Nowak, 1999; Leslie, 2011; Ramesh et al., 2012).

In the mosaic environment of Nam Lot, the importance of these intermediate and open zones as ecosystems rich in prey species, is supported by the hunting lifestyle of large predators. At Nam Lot, the spotted hyenas and dholes had access to a large spectrum of terrestrial prey species. Rhinoceroses were exclusive resources for hyenas, whereas wild pigs were most likely preyed upon by hyenas and dholes taking into account their highly probable abundance in this moist habitat-type (Bacon et al., 2015). The kill of juvenile rhinoceroses weighing up to 400 kg required obligate hunting in packs (of about 15 hyenas according to Kruuk, 1972) which could have been difficult in a closed forested vegetation. Observations made in Africa support this assumption. When the kills of hyenas involve the largest prey, buffaloes (200–400 kg, up to 13%) and elands (> 400 kg, up to 2%) in open savannas, hyenas hunt in large packs (Kruuk, 1972; Cooper et al., 1999; Höner et al., 2002). The difference with the MIS 5 equatorial ecosystem of Sibrambang of comparable age is particularly notable. At Sibrambang, predators had access to a more restricted spectrum of prey, among medium-sized mammals (Figs. 6, 1SI, 3SI, 4SI).

No reliable evidence supports for the moment the presence of

Table 1
Percentages of arboreal and mixed arboreal/terrestrial faunas in Asian sites.

Borneo		Sri Lanka	Vietnam
Niah cave (West Mouth)	Niah cave (Lobang Hangus)	Batadomba-Iena	Duoi U'Oi
~50–0.25 ka	~10 ka	~36–12 ka	~70–60 ka
31.8%	56.1%	82%	27.2%

NISP percentages of arboreal (monkey and ape) and mixed arboreal/terrestrial (squirrel, civet, and bear cat) faunas calculated for *Homo sapiens* sites: Niah cave, the Hell Trench of the West Mouth (data calculated from Table 1 in Barker et al., 2017); Niah cave, Lobang Hangus (data calculated from Fig. 5 in Piper and Rabett, 2009); Batadomba-Iena (data from Perera et al., 2011); and for the hominin Duoi U'Oi site (this paper).

modern humans during MIS 5 in northeastern Laos, before 70 ka. However, signs of an expansion in the time range of ~120–70 ka in South Asia (Petraglia et al., 2007; Armitage et al., 2011; Blinkhorn et al., 2013; Groucutt et al., 2015), as far as Java (Storm et al., 2005; Storm and de Vos, 2006; Westaway et al., 2007), and in central to south China (Liu et al., 2010a, 2010b, 2015; Cai et al., 2017; Shen et al., 2013; Bae et al., 2014), support the idea of multiple MIS 5 dispersal events.

In the plausible scenario that modern humans entered Southeast Asia during MIS 5, a Nam Lot-type habitat could have constituted a relatively attractive environment for people with small to large game available and exploitable on the ground. The presence of intermediate zones in rainforest environments, open forests, forest-edges, and grassland zones rich in prey species, could have procured many tuberous and leafy species for food (Hunt et al., 2012; Roberts et al., 2017a, 2017b).

4.2. MIS 4 environmental context in northern Vietnam

When comparing the Nam Lot fauna with that of Duoi U'Oi (70–60 ka), the climatic fluctuations between MIS 5 (~128–71 ka) and MIS 4 (~71–52 ka) did not seemingly modify the abundance of forest-dependent species, especially that of pigs and rhinoceroses. The MIS 4 biotope supported a large variety of small to large ungulates, including muntjac, wild pig, deer, tapir, rhinoceros, and elephant. Macaques remained much more abundant than orangutans (compared to more southern latitudinal sites such as Sibrambang; Table 1SI). In terms of biodiversity, the major climate-driven change observed in the Duoi U'Oi fauna is the absence of the largest ungulate species, *Stegodon orientalis*. The absence of the giant tapir (*Megatapirus augustus*) - recorded in most MIS 5 faunas in northern Indochina and southern China - is also notable (Cuong, 1985, 1992; Olsen and Ciochon, 1990; Wu and Poirier, 1995; Bacon et al., 2008a, 2011; Wang et al., 2007; Rink et al., 2008). The last Interglacial-glacial shift, characterized by changes in the intensity of the East Asian monsoon (Wang et al., 2008), was marked at the latitudes ~20°N by the onset of relatively cool and wet conditions (with ~4 °C cooler temperatures than present), that contributed to important changes in rainforest composition (Zheng and Lei, 1999). Perhaps, the forest-type of Duoi U'Oi could not support locally such high ungulate biomass, most likely correlated with the reduction of the low-light canopy area (ongoing isotopic analysis of the Vietnamese Duoi U'Oi fauna (70–60 ka) compared to that of Coc Muoi (148–117 ka) will allow us to test this hypothesis). Based on the vegetation component of the site, the area might be composed of more open forests, as suggests the low percentage (8%) of arboreal and shrub pollens, in comparison with that of non-arboreal and fern spores (56%) (Fig. 2SI). Furthermore, the abundance of the sambar deer, might also point to the presence of more extensive mixed and open areas, considering the flexibility of its diet by browsing or by grazing depending on the habitat (Leslie, 2011).

Nevertheless, this MIS 4 rainforest environment continued to guarantee a large spectrum of small to large terrestrial game. The presence of sympatric species within the large carnivore guild, such as tiger, leopard and dhole, is strong evidence for the abundance of prey-species, as well as their availability in different size classes, on the ground and in arboreal strata (Hayward et al., 2006, 2012, 2014, and references therein). Tigers, which were most likely the main predators at the site, prefer to hunt in wooded and open areas by stalking their prey.

At Duoi U'Oi, the foraging economy practiced by hominins most likely contained a great representation of terrestrial animals. The small representation of arboreal and semi-arboreal species which constitute 27.2% of the assemblage, differs from that of more recent sites (MIS 3–2), such as Niah cave in Borneo with 31.8% (~50 ka; Barker et al., 2007), and 56.1% at Lobang Hangus (Terminal Pleistocene; Piper and Rabett, 2009), in which the increase of hunted prey coincides with efficient hunting technologies, particularly with the use of bone technology. Another example comes from the settlement of *Homo sapiens* in the rainforest of inland Sri Lanka, at Batadomba-lena rockshelter (~36 ka to Holocene; Perera et al., 2011), where arboreal and semi-arboreal species < 20 kg constitute up to 82% of all animals recorded (Table 1). This procurement of diverse resources is associated with evidence of behavioral modernity (microlithic industries, composite tools, practice of symbolism, and ritual).

If there is growing evidence that hominins lived in Southeast Asian various rainforest contexts - *Homo sapiens* at Tam Pà Ling (~70–46 ka; Demeter et al., 2017; Shackelford et al., 2018) and Lida Ajer (73–63 ka; Westaway et al., 2017), and an unidentified hominin at Callao (~66.7 ka; Mijares et al., 2010), and Duoi U'Oi (70–60 ka; the present analysis) - there are no however direct evidence for the moment that they were using the rainforest, and their degree of reliance on these habitats remains to be demonstrated.

The lack of artefacts (made from bone, stone, antlers or plants, charcoal, ornaments, traps, and other kind of manifestations) associated with hominin remains in MIS 5–4 Indochinese sites is obviously an impediment to our understanding of their adaptive skills, and particularly those of the earliest modern humans when expanding into the Southeast Asia. At present, there is no evidence of any of the innovations described in the other sites of comparable age (McBrearty and Brooks, 2000; Norton and Jin, 2009; Petraglia et al., 2012; Kaifu et al., 2015; d'Errico et al., 2017; Bae, 2017), except the potential occupation within rock shelters rather than open-air sites in karstic landscapes, further inducing a lower probability for fossil preservation and/or discovery (Morley, 2017).

5. Conclusions

The Nam Lot isotopic results indicate a large range of coexisting habitats in northeastern Laos during MIS 5 with closed low-light tropical rainforests, “intermediate” rainforests, and C_3–C_4 open woodlands/‘savannas’. This woodland ecosystem - notably the “intermediate” rainforest - carried most of the ungulate biomass, with a variety of small to large-bodied ground-dwelling animals. The zooarchaeological data indicate a high degree of species interactions, as suggested by the presence of group-living predators.

The Duoi U'Oi zooarchaeological results also show that, during MIS 4, the locality constituted a relatively attractive environment for predators (hominins and non-hominins). The foraging economy practiced by hominins most likely contained a great representation of terrestrial animals.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2018.03.034.

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